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one competent to criticize his results in any detail. All we can say is that we recognize the same lucidity and fullness of treatment, and the same broadly philosophical point of view, which have long been familiar in the writings of the author on Mollusca. Adding to this the beautiful and abundant illustrations, it seems that there is nothing left to be desired.

To the general zoologist, perhaps the most interesting part will be that in which the work of Darwin on barnacles is reviewed. Darwin wrote about sixty years ago, and to-day Dr. Pilsbry has this to say of his work:

"His grasp of detail was so comprehensive and his language so lucid that one can not expect to improve upon them. In the field he covered one can not do better than to imitate. Yet it has been possible to extend the work in certain directions."

"His monograph on the subclass Cirripedia is one of the most brilliant morphologo-systematic studies to be found in the whole field of systematic zoological literature."

Under *Balanus* (p. 50) we read:

"It is a remarkable testimony to Darwin's insight and restraint that every one of the species of *Balanus* admitted by him is still accepted as valid."

Under Coronulinæ (p. 269):

"We owe to him a discussion of the morphology of the group so lucid that no subsequent student has been able to add anything of importance."

Under Chthamalidæ (p. 292):

"We owe the establishment of this family solely to the taxonomic genius of Darwin, who first brought the genera together and demonstrated their relationship. I have examined and dissected many more species, I suppose, than any one else, and I find all of the evidence supports Darwin's views."

Thus, had Darwin never been known as a great philosophical naturalist and evolutionist, he would still have stood in the front rank as a brilliant taxonomist and morphologist.

One of the important facts brought out by Dr. Pilsbry is that the so-called cosmopolitan barnacles, when belonging to the littoral or shallow-water fauna, present numerous subspecies which conform in general to the faunal provinces already recognized for other marine animals. In general, also, the distribution of species is more restricted than has been supposed, as it is found that many of the records are taken from specimens attached to ships, far out of their natural range.

It appears that the British Museum, which contains Darwin's types and the *Challenger* materials, has the most important collection of barnacles in existence. Second to this is the U. S. National Museum, which possesses no less than 76 types.

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September 3, 1916

SPECIAL ARTICLES

ANTAGONISTIC SALT ACTION AS A DIFFUSION PHENOMENON

1. THE writer pointed out in 1905[1] that the antagonization of the toxic action of NaCl by $CaCl_2$ (or in general of salts with univalent cation by small quantities of a salt with bivalent cation) was due to the Ca preventing the diffusion of the NaCl through the membrane of the cell. It is often difficult to decide whether or not the antagonistic salt action is a diffusion phenomenon or a phenomenon due to the action of the salt upon the living protoplasm. We possess, however, one object in which definite proof can be furnished that the antagonistic salt action is merely a diffusion phenomenon, due to a direct action of one (or both salts) on the membrane and not on the protoplasm; namely, the egg of *Fundulus*. In this case the embryo is the living protoplasm and by comparing the action of salts on the egg, while the embryo is still inside, with the action of the same salts when the embryo is freed from the membrane, we can make sure that the phenomena of antagonization observed in the egg of *Fundulus* are diffusion phenomena. This may be illustrated by a few simple examples.

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[1] Loeb, J., *Arch. ges. Physiol.*, 1905, CVII., 252.

In his paper of 1905 the writer pointed out already that $ZnSO_4$ retards the injurious action of a *m*/2 or 5/8 *m* solution of NaCl upon the embryo inside the egg, while the newly hatched fish dies more rapidly in a *m*/2 or 5/8 *m* NaCl solution when a trace of $ZnSO_4$ is added; and that this fact was only comprehensible on the assumption that the antagonistic action of the $ZnSO_4$ in the former case was due to an action of this salt upon the membrane, whereby the rate of diffusion of the NaCl through the membrane was diminished.

When we put eggs of *Fundulus* from six to ten days old into a 3 *m* NaCl solution the embryos are killed and coagulate inside of five hours, for the reason that in this concentration the NaCl is able to diffuse through the membrane, which is practically impermeable to water as well as to balanced salt solutions of not too high a concentration. When we add 1 c.c. 10/8 *m* $CaCl_2$ to 50 c.c. 3 *m* NaCl, the embryo will keep alive (as indicated by the continuation of heartbeat, circulation, and spontaneous motions of the whole embryo) for from three to five days.[2] This prolongation of life through the addition of Ca is due not to an action upon the protoplasm but to a prevention of the diffusion of the NaCl into the egg, since if we take the embryo out of the egg (or use the newly hatched embryo) it is killed in 50 c.c. 3 *m* NaCl + 1 c.c. 10/8 *m* $CaCl_2$ inside of a few minutes. The antagonistic effect of the $CaCl_2$ consisted therefore in this case in the Ca modifying the egg membrane in such a way as to retard the diffusion of NaCl through the membrane. Since the objection might be raised against this conclusion that a slow diffusion of Ca into the egg counteracted the effects of an almost equally slow diffusion of NaCl upon the fish itself, we may add that the experiment succeeds just as well if the $CaCl_2$ is replaced by $MnCl_2$, which is not able to counteract the injurious action of NaCl upon the embryo outside the egg, while it counteracts the injurious action of NaCl upon the embryo while the latter is inside the egg. The antagonistic action of Ca or Mn or $ZnSO_4$ (or any salt with bivalent cation) upon the injurious action of a NaCl solution consists, therefore, in the case of the egg of *Fundulus*, purely in the prevention or retardation of the diffusion of NaCl through the membrane of the egg.

KCl is a general nerve and muscle poison and causes cessation of the heartbeat in comparatively low concentrations. When we put the eggs of *Fundulus*, after heartbeat and circulation are established, directly from sea-water into *m*/8 KCl the hearts stop beating in a few hours. If, however, the *m*/8 KCl solution is made up in *m*/1 NaCl + $CaCl_2$ the embryo may live in the solution for ten days or more. That we are dealing in this case of antagonism also with a diffusion phenomenon is made certain by the fact that the combination $NaNO_3 + MnCl_2$ is practically as good an antagonist against KCl as is $NaCl + CaCl_2$, as long as the embryo is in the egg; while when it is out of the egg the mixture $NaNO_3 + MnCl_2$ (as well as $NaNO_3$ or $MnCl_2$ alone) is unable to antagonize KCl.

These examples, to which many others might be added, show that the phenomena of antagonism described by the writer for the egg of *Fundulus* are purely diffusion phenomena and due to a direct action of the salts on the membrane of the egg and not due to an action of the salts upon the protoplasm of the embryo.

2. The experiments on the egg of *Fundulus* give us therefore an unusual advantage, inasmuch as they allow us to decide with certainty whether the phenomena of antagonism are diffusion phenomena or phenomena due to the action of salts upon the protoplasm; since we can easily separate the protoplasmic part of the egg—the embryo—from the membrane. On account of this unusual advantage the writer has made this object the basis of his work on the theory of physiologically balanced solutions. When we deal with cells whose membranes we can not remove at desire we have a reason to doubt whether or not the phenomena of antagonistic salt action are also of the order of diffusion phenomena. The observations of the writer on the fish itself seem to indicate that phenomena of diffusion enter

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[2] Loeb, J., *Biochem. Ztschr.*, 1912, XLVII., 127.

here just as well, since there is a far-reaching parallelism between the rules of antagonism for the isolated fish and the egg. Thus Loeb and Wasteneys have shown that the fish *Fundulus* dies more slowly in a pure $m/100$ or $m/50$ KCl solution than when 10 molecules of NaCl are added to 1 molecule of KCl; while the toxic action of KCl is prevented when 17 or more molecules of NaCl are added to 1 molecule of KCl.[3] The writer has recently found that the same fact is true for the eggs of *Fundulus,* with this difference only, that much higher concentrations of KCl are required to demonstrate the phenomenon in the egg than in the fish; and that a much wider range of antagonistic salts can be used in the case of the egg than in that of the fish. This difference, however, can easily be accounted for by the difference between the membrane of the egg and the skin of the fish.

The fact that the stimulating action of salts upon nerve and muscle is inhibited by Ca may also be due to the prevention of the diffusion of the stimulating salts into the nerve or muscle by the Ca.[4]

The writer is in no position to state whether or not Osterhout's[5] interesting observations on the electric conductivity of *Laminaria* may be interpreted as diffusion phenomena, since it is not possible in that object to separate the direct action of the salts on the membrane from that upon the protoplasm. The death of a cell under the influence of a salt must be ascribed to an action of the salt upon the protoplasm, but this action can only take place after the salt has been able to diffuse through the membrane.

The diffusion of certain electrolytes through a membrane seems to depend in addition to the osmotic pressure of the salt in solution upon a second effect which the writer has called the general salt effect.[6] This effect he attributes to a combination of the salt with certain constituents of the membrane, presumably proteins.

3. There are certain kinds of antagonism which seem peculiar to phenomena of irritability and which can not be found in phenomena of diffusion. Thus the larvæ of the barnacle are unable to swim when put into a mixture of $NaCl + KCl + CaCl_2$ until some $MgCl_2$ is added; they are also unable to swim in a mixture of $NaCl + KCl + MgCl_2$ without $CaCl_2$.[7] It is not strictly correct to call this a case of antagonism between Ca and Mg, since in mixtures of $CaCl_2$ and $MgCl_2$ (without $NaCl + KCl$) the animals are no more able to swim than in a mixture of NaCl and KCl alone or of $NaCl + KCl + MgCl_2$. Either Ca or Mg suffices to counteract the diffusion of $NaCl + KCl$ through the membrane of *Fundulus,* and it is not necessary to add both. The writer had first observed this type of antagonism in the rhythmical contractions of the jellyfish *Polyorchis*[8] and it was afterwards observed by Meltzer and Auer in mammals.[9] It may be peculiar to special sense organs or other animal structures since the writer was not able to observe it in *Euglena.*

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THE ELECTRICAL CONDUCTIVITY OF SOLUTIONS AT DIFFERENT FREQUENCIES

V.[1] ON THE MEASUREMENT OF THE TRUE AND APPARENT ELECTRICAL CONDUCTIVITIES AND THE INDUCTANCE, CAPACITY, FREQUENCY AND RESISTANCE RELATIONS

For the past two years the authors have been engaged in a detailed study of the passage of alternating currents at different frequencies through solutions of electrolytes. For a source of current we have used several generators but especially the Type *B* Vreeland

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[3] Loeb, J., and Wasteneys, H., *Biochem. Ztschr.,* 1911, XXXII., 155.

[4] Loeb, J., and Ewald, W. F., *Jour. Biol. Chem.,* 1916, XXV., 377.

[5] Osterhout, W. J. V., Science, 1916, XLIV., 395.

[6] Loeb, J., *Proc. Nat. Acad. Sc.,* 1916, II., 511.

[7] Loeb, J., *Jour. Biol. Chem.,* 1915, XXIII, 423.

[8] Loeb, J., *Jour. Biol. Chem.,* 1905–06, I., 427.

[9] Meltzer, S. J., and Auer, J., *Am. Jour. Physiol.,* 1908, XXI., 400.

[1] Summary of a paper given at the Urbana meeting of the American Chemical Society, April 18, 1916.